

Implications of life-history invariants for biological reference points used in fishery management

Erik H. Williams and Kyle W. Shertzer

Abstract: Fish harvest policies typically rely on biological reference points for measures of a stock's status. We examine three common biological reference points based on fishing mortality rates corresponding to maximum sustainable yield with an age-structured deterministic model. We incorporate invariant life-history relationships into the model to maintain parsimony and focus model parameters on biologically plausible parameter space. A wide range of biological and fishery characteristics were used in the model so that our results pertain to the management of virtually any exploited population. Results indicate that two biological reference points based on spawning biomass are insensitive to life-history parameters, whereas one based on natural mortality is highly sensitive. All three depend largely on the choice of a stock–recruitment function and on steepness, a measure of the population growth rate. For each of the three, values have been previously proposed that were intended to safely apply to all fisheries; our results show that no such universal values exist. We recommend determining stock–recruitment functions a priori, establishing biological reference points on steepness explicitly and eliminating harvest policies based on the natural mortality rate altogether.

Résumé : Les politiques de récolte de poissons se basent généralement sur des points de référence biologiques comme mesures du statut d'un stock. Nous examinons ici trois points de référence biologiques d'usage courant, qui sont basés sur des taux de mortalité dus à la pêche correspondant au rendement équilibré durable, à l'aide d'un modèle déterministe structuré d'après l'âge. Nous incorporons au modèle des relations invariables du cycle biologique pour maintenir la parcimonie et nous maintenons les paramètres du modèle dans un espace de vraisemblance biologique. Une gamme étendue de caractéristiques biologiques et halieutiques est utilisée dans le modèle, si bien que nos résultats s'appliquent à presque toute population exploitée. Nos résultats indiquent que les deux points de référence biologiques basés sur la biomasse des géniteurs sont insensibles aux paramètres du cycle biologique, alors que l'autre basé sur la mortalité est très sensible. Tous les trois dépendent fortement du choix de la fonction stock–recrutement et de l'inclinaison, une mesure du taux de croissance de la population. Pour chacun des trois, on a proposé dans le passé des valeurs qui permettaient de les appliquer sans problème à toutes les pêches; nos résultats démontrent que de telles valeurs universelles n'existent pas. Notre recommandation est d'établir a priori les fonctions stock–recrutement, de baser les points de référence biologiques explicitement sur l'inclinaison et d'éliminer complètement les politiques de récolte basées sur la mortalité naturelle.

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Introduction

Biological reference points (BRPs) are used in marine fishery management to set harvest policies. They serve as either a target of management (target reference point) or a limit of exploitation (limit reference point). Distinction between target and limit allows precautionary management in the sense of maximizing harvest while protecting the spawning potential of the stock (Prager et al. 2003).

In the role of target, BRPs are a proxy for optimal harvest when data restrictions preclude direct estimation. In the role of limit, BRPs are a harvest threshold not to be exceeded. For either role, numerous BRPs have been proposed, typically based on fishing mortality rate (F) or some measure of abundance such as spawning stock biomass (SSB) or spawn-

ing stock biomass per recruit (SSBR) (Quinn and Deriso 1999).

One common BRP relates the target or limit fishing mortality rate (F') to the natural mortality rate (M) by some constant c_1 such that $F' = c_1 M$. The rationale of this “ M -based” BRP is that stocks with higher M tend to have higher production rates and can therefore sustain increased fishing. It was originally proposed that $F' = M$ as a proxy for the maximum sustainable fishing rate (F_{MSY}). Current applications usually take a more risk-averse strategy by considering M an upper bound and using $c_1 < 1$ (Quinn and Deriso 1999). For example, groundfish harvest policies for the Pacific and North Pacific (PFMC) councils use $F' = 0.75M$ in cases when limited data do not allow reliable estimation of F_{MSY} (Witherell and Ianelli 1997; PFMC 2001). The rationale is of

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A second common BRP is based on biomass, labeled here the “ B -based” BRP. The goal is to define F' such that the corresponding equilibrium biomass is a fixed fraction c_2 of the unfished biomass, $SSB_{F=F'}/SSB_{F=0} = c_2$. The ratio measures the impact of fishing on the stock's potential biomass. A larger ratio implies a stock less affected by fishing. Under simple logistic population growth (e.g., Graham-Schaefer model), the c_2 corresponding to SSB at F_{MSY} is 0.5. For the Beverton–Holt and Ricker stock–recruit functions, the c_2 corresponding to SSB at F_{MSY} is ≤ 0.5 (Ricker 1975). The Pacific Fishery Management Council uses a target B -based BRP of $c_2 = 0.4$ for their groundfish harvest policy (PFMC 2001).

A third common BRP is the spawning potential ratio (SPR; Gabriel et al. 1989; Goodyear 1993). SPR is the spawning stock biomass per recruit of a fished population relative to that of an unfished population. As before, the goal is to define F' such that the BRP equals some fixed fraction c_3 . The SPR is then $SSBR_{F=F'}/SSBR_{F=0} = c_3$. Lower values of c_3 correspond to reduced spawning potential at higher fishing rates. Several analyses have considered potential values of c_3 for general applicability to many fisheries. Clark (1991) analyzed values of c_3 over a range of biological and fishery parameters for New England groundfish and determined $c_3 = 0.35$ would maintain sufficient spawning biomass levels and could serve as a management target. The target value was subsequently revised to $c_3 = 0.3$ by Mace and Sissenwine (1993) and $c_3 = 0.4$ based on analyses by Clark (1993) and Mace (1994). For West Coast groundfish, it appears that c_3 values as high as 0.5 are more appropriate as a management target (Clark 2002; Dorn 2002; Myers et al. 2002).

The three BRPs above, although based on different metrics (F , SSB, or SSBR), are not independent. They are related by the biology of the stock. For example, targeting F as a percentage of natural mortality has consequences for SPR in ways that depend on life-history traits. However, management typically uses a BRP without considering the implications for other potential BRPs and often unavoidably so when life-history data are limited.

In this paper, we use life-history theory to examine general applicability of the three common BRPs: M based, B based, and SPR. According to life-history theory, the evolution of demographic parameters is shaped by trade-offs (Stearns 1992). Energy allocated toward one function is energy not allocated toward another. For example, increased reproductive output may come at the cost of decreased survival. Such evolutionary constraints underlie a solid body of literature indicating invariant relationships between life-history parameters (overview in Charnov 1993). By building life-history invariants into models of stock dynamics, we are able to explore the robustness of and connections between the three harvest policies.

Our goals are to address three key questions regarding the link between life histories and BRPs corresponding to F_{MSY} . First, how are each of the BRPs constrained by invariant life-history relationships? Or conversely, once a harvest rate is specified, what does it imply about the underlying life-history parameters necessary to support it? It would be useful to know if a specific management strategy can be supported over a wide range of life histories, and if not, to which life-history parameters the strategy is most sensitive. Such information could help focus data collection. Second, how do the various harvest policies interrelate? For a given set of biological parameters, implementing a particular level of one harvest strategy automatically implies levels of the others. Commonly suggested levels may not be compatible among BRPs. Third, how sensitive are our results to deviations from the invariant life-history relationships? Although such relationships are evident across stocks, they may not describe any single stock well. A good harvest strategy should be robust to deviation from the expected life-history patterns. We explore answers to the above questions over ranges of the life-history strategy, steepness in the stock–recruit relationship, selectivity pattern, and timing of selection relative to maturity. The implications of our results apply generally to the management of virtually any stock.

Materials and methods

Model of stock dynamics

We simulate stock dynamics using a continuously structured catch-age model, similar to “dynamic pool” models standard in fishery management (e.g., Sissenwine and Shepherd 1987; Thompson 1992). A cohort of age $a = 0$ is initialized with N_0 individuals. As the cohort ages, the number of individuals in that cohort $N(a)$ decreases continuously owing to fishing (F) and natural mortality (M) rates,

$$(1) \quad \frac{dN(a)}{da} = -[M + Fs(a)]N(a)$$

where $s(a)$ is the age-dependent selectivity of fishing methods. We assume deterministic dynamics, which leads to a stable age structure in this model. Thus over the course of an individual's lifetime, integration with respect to age is equivalent to integration with respect to time. Given initial conditions $N(0) = N_0$, integration projects the number of individuals to any given age a :

$$(2) \quad N(a) = N_0 \exp(-Ma - F \int_0^a s(x)dx)$$

where x is a dummy variable of integration. Further integration across all ages provides the total yield obtained from a single cohort:

$$(3) \quad C = \int_a F s(a) N(a) da$$

In typical catch-age models with discrete age classes and constant age-specific selectivity, a discrete version of eq. 3 is solved by applying the Baranov catch equation across ages (Quinn and Deriso 1999). Here that is not possible because of the continuous age structure and selectivity. Instead, we

solve eq. 3 by numerical integration, feasible after specifying a selectivity function.

We use a logistic model of selectivity, chosen for its ability to depict a suite of selectivity patterns:

$$(4) \quad s(a) = \frac{1}{1 + \exp[-\eta_s(a - a_1)]}$$

Parameter η_s is the slope of the selectivity function, which controls the rate that selectivity approaches full selection (i.e., $s(a) = 1$) with age. Parameter a_1 is an inflection point that controls where $s(a) = 0.5$. In an age-structured population, selectivity relative to maturation can strongly influence F_{MSY} . We therefore express a_1 in terms of the age at maturity (a_{MAT}) shifted by a scaling parameter (τ) such that $a_1 = \tau a_{MAT}$. The parameter τ serves as a focus for analyzing the BRPs with respect to the timing of selection relative to age at maturity. For logistic selectivity, the solution to the integral of eq. 2 is

$$(5) \quad \int_0^a s(x)dx = \frac{-\eta_s a' + \log(1 + \exp[\eta_s a']) + \eta_s a'' - \log(1 + \exp[\eta_s a''])}{\eta_s}$$

where $a' = \tau a_{MAT} - a - 0.5$ and $a'' = \tau a_{MAT} - a + 0.5$ (Beyer 1978).

The age at maturity is defined here as the age when 50% of the individuals are mature. The proportion of mature individuals in a cohort $m(a)$ also follows the logistic model

$$(6) \quad m(a) = \frac{1}{1 + \exp[-\eta_m(a - a_{MAT})]}$$

where η_m controls the rate of maturation.

The length (L) of survivors increases with age according to the von Bertalanffy growth equation (von Bertalanffy 1938):

$$(7) \quad L(a) = L_\infty[1 - \exp(-Ka)]$$

where K is the Brody growth coefficient and L_∞ is the asymptotic length. We assume for simplicity that $L(0) = 0$ and that weight at age is proportional to length cubed ($W(a) \propto L(a)^3$). Hence the spawning stock biomass (SSB) is

$$(8) \quad SSB = \int_a N(a)m(a)W(a)da$$

The number of fish at age 0 in a cohort (N_0) is determined by equilibrium recruitment (R_{eq}) from a Beverton–Holt or Ricker stock–recruit function. Following convention, we parameterize the stock–recruit functions in terms of the level of unfished recruitment (R_0) and steepness (h). The parameter R_0 is the recruitment that occurs at the carrying capacity, defined by the intersection of the stock–recruit curve and the replacement line. Replacement occurs where recruitment exactly supplants the spawning biomass (i.e., line with slope equal to ϕ_0 , the spawning biomass per recruit at $F = 0$). The Beverton–Holt parameterization is

$$(9) \quad R = \frac{0.8R_0hSSB}{0.2\phi_0R_0(1-h) + (h-0.2)SSB}$$

where R is recruitment. Similarly, the Ricker parameterization is

$$(10) \quad R = \frac{SSB}{\phi_0} \exp \left[h' \left(1 - \frac{SSB}{R_0\phi_0} \right) \right]$$

A standard assumption in fishery modeling, adopted here, is that all density dependence in population dynamics can be described by the stock–recruit function.

In eq. 9, h refers to the proportion of R_0 that would be produced by 20% of the unfished spawning biomass (SSB₀; i.e., the carrying capacity) and ranges from 0.2 to 1.0 (Mace and Doonan 1988; Haddon 2001; Myers et al. 2002). In the Ricker stock–recruit function of eq. 10, h' does not have the same meaning because maximum recruitment may exceed R_0 and therefore h' ranges from zero to infinity (Kimura 1988; Dorn 2002). Under equilibrium conditions and assuming that $R_0 = K$, the Beverton–Holt and Ricker steepness parameters are related to the maximum reproductive rate λ and the intrinsic growth rate r (Quinn and Deriso 1999; McAllister et al. 2001; Myers et al. 2002),

$$(11) \quad \lambda = \exp(r) = \frac{4h}{(1-h)} = \exp(h')$$

We note that the “4” in eq. 11 is a result of defining h with the arbitrary choice of 20% of SSB₀. It could be eliminated if h were redefined using 50% of SSB₀, which would result in more elegant solutions of steepness’ relationships to other population parameters (Kimura 1988).

Using the convention of 20%, the equilibrium recruitment R_{eq} corresponding to a given F is

$$(12) \quad R_{eq} = R_0 \left[\frac{0.8hSPR - 0.2(1-h)}{SPR(h-0.2)} \right]$$

for the Beverton–Holt function. For the Ricker function, the analogous equation is

$$(13) \quad R_{eq} = \frac{R_0}{SPR} \left(1 + \frac{\log SPR}{h'} \right)$$

In eqs. 12 and 13, SPR is the spawning potential ratio defined previously.

Life-history invariants

The above model contains three biological parameters that drive, and are shaped by, evolution: natural mortality M , the growth coefficient K , and age at maturity a_{MAT} . Correlations among these parameters are well documented in comparative life histories (Stearns 1992; Charnov 1993). As the result of trade-offs between reproduction and survival, species with relatively high natural mortality tend to grow quicker and mature younger; conversely, species that devote less energy toward growth and gonad development tend to suffer lower natural mortality (Roff 1984; Jensen 1996). Although many different life-history strategies exist, certain combinations of life-history parameters can be expressed as dimensionless quantities that have been shown to be invariant across a wide range of taxa (Charnov 1993).

One such dimensionless quantity is M/K . Charnov (1993) analyzed the relationship between M and K by applying or-

dinary regression to a data set (Pauly 1980) of 175 fish stocks from around the world representing 40 families and 110 species. The data display broad scatter, but Charnov (1993) found the mean relationship to be nearly constant:

$$(14) \quad M/K \equiv 1.65$$

Beverton (1992) provided a theoretical relationship among life-history parameters M , K , and a_{MAT} based on the dimensionless ratio of length at maturity to asymptotic length. Beverton (1992) reported two expressions for that ratio: $L(a_{\text{MAT}})/L_{\infty} = 3/(3 + M/K)$ from Holt (1958) and $L(a_{\text{MAT}})/L_{\infty} = 1 - \exp(-Ka_{\text{MAT}})$, the ratio expected from von Bertalanffy growth. By equating the right-hand sides of the two expressions, one can solve for a_{MAT} as a function of M and K :

$$(15) \quad a_{\text{MAT}} = \log \left(\frac{3K + M}{M} \right) / K$$

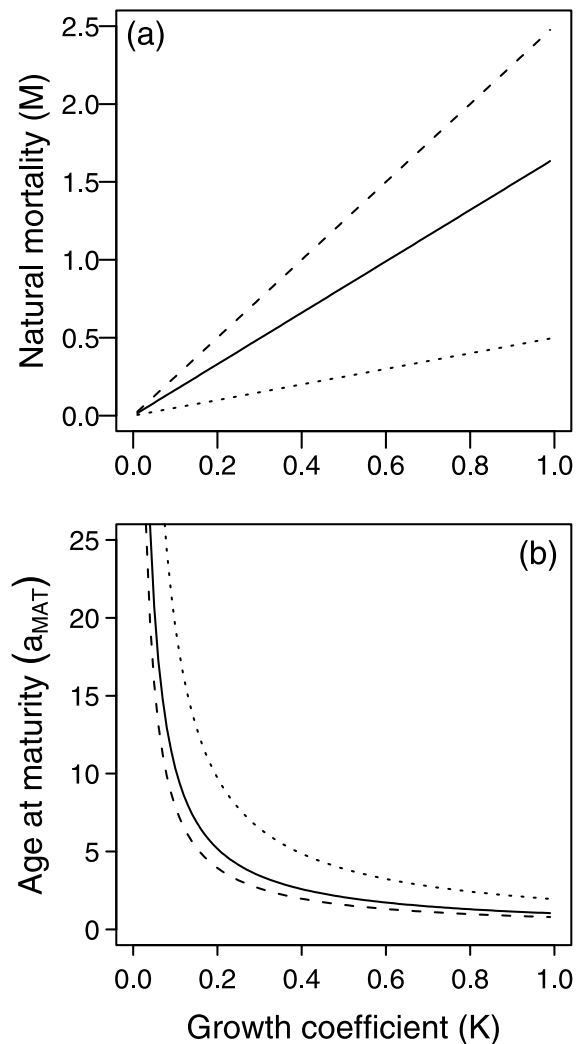
Equation 15 requires the assumption that age at maturity occurs so as to maximize lifetime egg production (Beverton 1992).

Analyses

To analyze the three BRPs for relevance to many fisheries, we apply the model over a broad range of biological and selectivity patterns. For each combination of parameters, we use Shepherd's method to determine F_{MSY} (Shepherd 1982). The method searches iteratively for a solution of F that maximizes yield (eq. 3) under a given stock–recruit curve and a stable age structure. Catch, numbers, and spawning biomass are computed over ages 0 to a maximum defined as the age when a negligible percent (1×10^{-6}) of the cohort survives. Once deemed a target, F_{MSY} is now more often considered a limit reference point (Mace 2001). Based on $F = F_{\text{MSY}}$, we compute corresponding values of the three BRPs (i.e., c_1 , c_2 , and c_3). In actual fishery management, the method is reversed: c_i 's are set first and the corresponding F serves as a proxy for the unknown F_{MSY} . Our analyses identify the BRP values where such proxies are reliable.

In our analyses, we systematically vary biological parameters of steepness (h or h') and growth (K). For each value of K , the life-history invariant relationships (eqs. 14 and 15) provide values of M and a_{MAT} . We also systematically vary fishery parameters controlling the selectivity pattern (η_s) and the timing of selection relative to age at maturity (τ). Parameter η_s takes on three different values. An extreme value ($\eta_s = \infty$) represents selectivity that changes from zero to one almost instantaneously with age ("knife-edged" selection). A low value ($\eta_s = 0.5$) represents selectivity that increases slowly over a wide range of ages. A moderate value ($\eta_s = 3.0$) represents an intermediate selectivity. We assume that selectivity increases with age at the same rate as maturation ($\eta_s = \eta_m$), justified by noting that selectivity as it relates to availability and maturation are typically linked by migration patterns or size-at-age distributions. As with η_s , τ takes on three different values. The values represent selection before ($\tau = 0.75$), at ($\tau = 1.0$), or after ($\tau = 1.25$) the age when 50% of the cohort is mature. For all combinations of biological

Fig. 1. Relationships of (a) natural mortality M and (b) age at maturity a_{MAT} to the von Bertalanffy growth parameter K using three values of M/K : 2.5 (broken line), 1.65 (solid line), and 0.5 (dotted line).



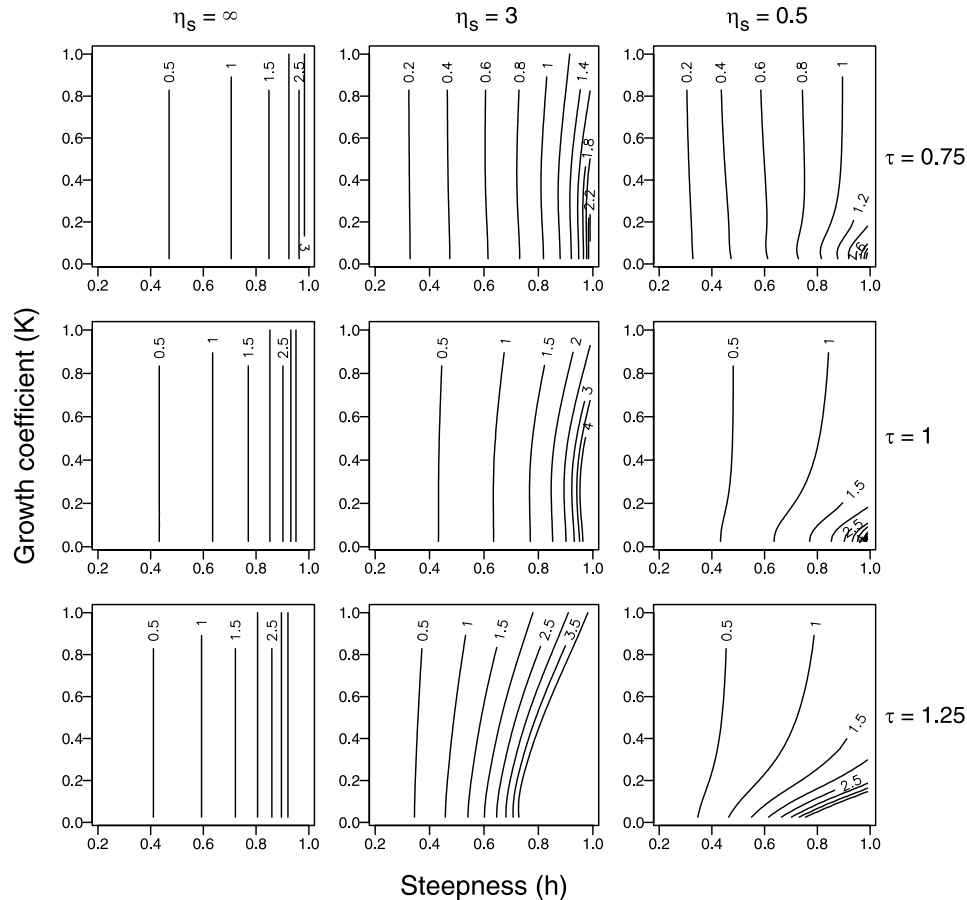
and fishery parameters, we examine values of and relationships between the three BRPs at $F = F_{\text{MSY}}$.

A key consideration is how sensitive the above results are to the underlying M/K ratio. Charnov's fitted ratio (Charnov 1993) of $M/K = 1.65$ describes the "average stock", but this does not necessarily fit well for any given stock. Depending on the estimation scheme, Charnov (1993) reported a M/K range of 1.6 to 2.1. Beverton (1992) suggested a lower bound closer to 0.5, based on a different data set. We conservatively consider wide deviation from the "average stock", using a low ratio of $M/K = 0.5$ and a high ratio of $M/K = 2.5$ (Fig. 1a). Such a range should approximate the gamut of plausible M/K ratios, and it creates a corresponding range of values for age at maturity (Fig. 1b).

Results

The use of life-history invariants allows each BRP to be viewed as a function of the growth coefficient (K) and steepness (h or h'). The values from the M -based policy are illustrated in Fig. 2. In the case of knife-edged selection and

Fig. 2. Values of the M -based biological reference point (up to 4.0 only) using the Beverton–Holt stock–recruit function and an M/K ratio of 1.65. Rows correspond to values of τ , the ratio of the age at 50% selectivity to the age at 50% maturity, and columns correspond to values of η_s , the slope of selectivity.



maturity, the M -based BRP depends only on steepness (Fig. 2, left column). However, with a shallower slope in the selection curves, the BRP depends on both K and h nonlinearly, particularly at higher levels of steepness (Fig. 2). For any given slope, the shift (τ) in selection relative to maturity affects the BRP value. As τ increases, the BRP tends to increase for similar values of steepness (Fig. 2).

The B -based and SPR BRPs exhibit patterns similar to those of the M -based BRP: knife-edged selection results in BRP values that are independent of K , and shallower-sloped selection results in values that depend nonlinearly on both K and h (Figs. 3 and 4). However, unlike the M -based BRP, the B -based and SPR BRPs are hardly influenced by τ . With increased τ , there is no change in either BRP for steepness smaller than ~ 0.7 , and only a slight reduction otherwise (Figs. 3 and 4).

The analyses show that among the three BRPs, the M -based policy depends most on fishery and life-history parameters, whereas SPR depends least (Figs. 2, 3, and 4). Only at the highest steepness values (>0.7) does SPR begin to depend on life-history parameters (M , K , a_{MAT}) represented by K (Fig. 4). However, all three BRPs are highly dependent on steepness (Figs. 2, 3, and 4).

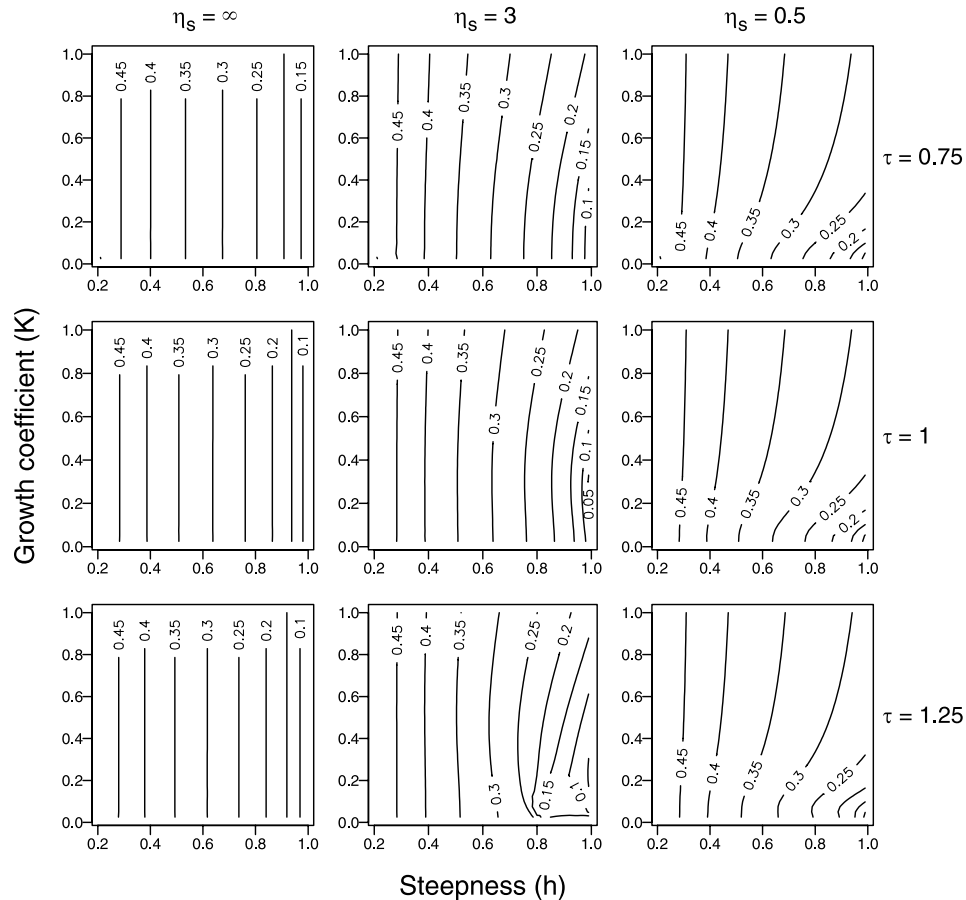
All three BRPs under the Ricker stock–recruit function (not shown) exhibit qualitatively similar patterns as under

the Beverton–Holt. SPR under the Ricker is highly dependent on steepness and nearly independent of the life-history parameters summarized by K . Again, there is some dependence on K at the highest steepness values, but a weaker dependence under the Ricker function than the Beverton–Holt.

Plotting the BRPs against one another, over the full range of fishery and life-history parameters, reveals their interrelationships (Fig. 5). For each selectivity pattern, the B -based and SPR BRPs have a tight relationship, a result of their independence from life history. The relationships are not nearly as tight between the M -based BRP and either of the other two, particularly for selectivities other than knife-edged. These results indicate that the B -based and SPR BRPs are compatible over a broad range of fishery and life-history parameters, whereas neither is so compatible with the M -based policy.

The relationship between the B -based and SPR BRPs appears to be quite strong (Fig. 5); however, that result is limited to the Beverton–Holt stock–recruit function and a single value of $M/K = 1.65$. A fuller examination using both the Beverton–Holt and Ricker functions and several M/K ratios indicates more variability (Fig. 6). Nonetheless, the relationship remains fairly consistent for each stock–recruit function, particularly in the case of knife-edged selection. Other than for the highest BRP values, the relationship depends

Fig. 3. Values of the B -based biological reference point using the Beverton–Holt stock–recruit function and an M/K ratio of 1.65. Rows correspond to values of τ , the ratio of the age at 50% selectivity to the age at 50% maturity, and columns correspond to values of η_s , the slope of selectivity.



considerably on the underlying stock–recruit function. Given similar population parameters, the Ricker function tends to produce higher B -based values and lower SPR values than does the Beverton–Holt function. As suggested in Fig. 6, the commonly assumed SPR proxy of $F_{40\%}$ would result in SSB levels near 30 and 40% of unfished levels for the Beverton–Holt and Ricker functions, respectively.

The BRP values can be fairly sensitive to the M/K ratio, shown here for the selectivity pattern with intermediate slope (Fig. 7). By using low and high extremes of the M/K ratio, Fig. 7 presents the full variability in BRP values due to deviations from the expected life histories. The M -based values show the greatest sensitivity to deviations in M/K for both Beverton–Holt and Ricker stock–recruit functions. The B -based values appear moderately sensitive, with greater variability under the Ricker function than under Beverton–Holt. The SPR values are by far the most robust to deviations in M/K for both stock–recruit functions.

The BRP values are more sensitive to deviations in M/K when the selectivity pattern has a shallower slope (not shown). When selectivity is knife-edged, the values change little or not at all with deviations in the M/K ratio (Fig. 8). Again, SPR is the most robust, with the B -based BRP a close second. Furthermore, the previous result that τ does not affect SPR values holds across the full range of M/K ratios.

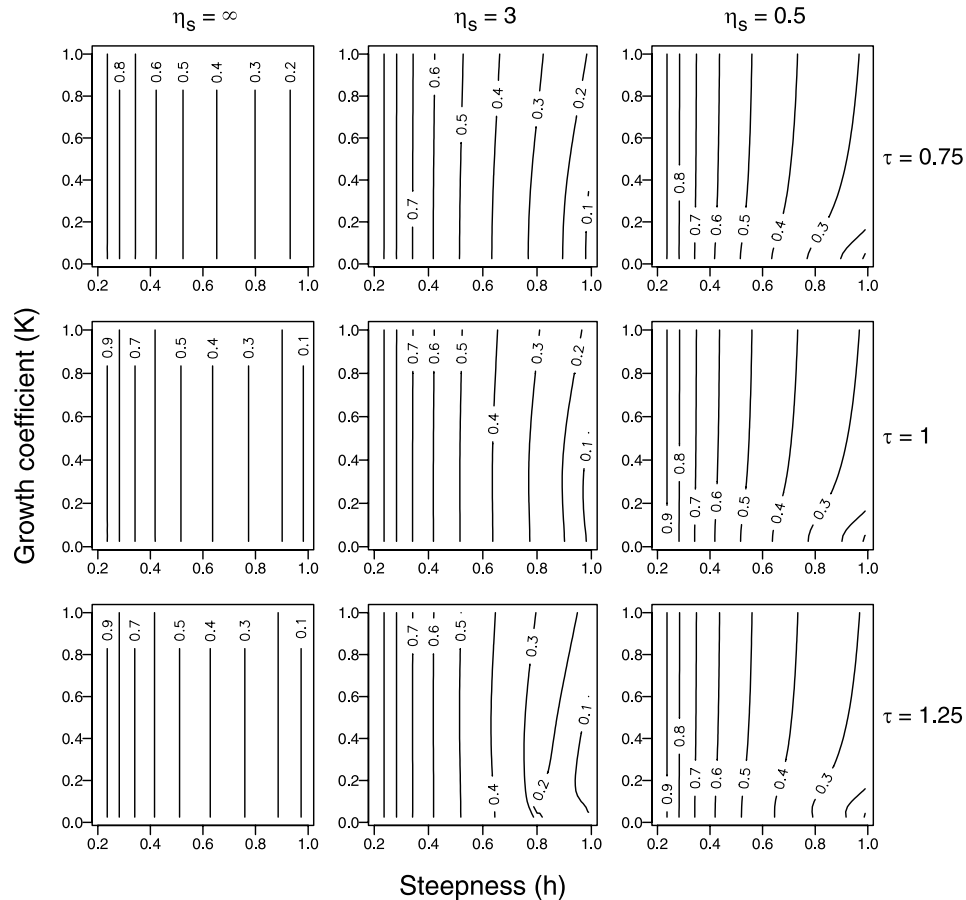
Scaling the Ricker steepness (h') to the Beverton–Holt steepness (h) elucidates how choice of the stock–recruit function affects the BRPs (Fig. 9). For each BRP, values under the two functions are nearly identical at low steepness and diverge as steepness increases. For a given steepness, the Beverton–Holt function produces higher SPR values and lower B - and M -based values. The management implication is that for a given population growth rate, a stock with Ricker recruitment can support a higher rate of exploitation than can one with Beverton–Holt recruitment.

Discussion

We have used a population model based on invariant life-history relationships to analyze common fish harvest policies. Life-history invariants have a solid theoretical basis (Roff 1984; Beverton 1992; Charnov 1993) and have been valuable in other fishery applications (Mangel 1996; Charnov and Skuladottir 2000; Frisk et al. 2001). Our use of them has allowed insights to emerge about biological reference points, particularly regarding their relations to life-history parameters and each other. Many of these insights carry strong implications for management.

Previous studies have drawn connections between BRPs and life-history parameters. Mace (1994) examined several

Fig. 4. Values of the spawning potential ratio, SPR, biological reference point using the Beverton–Holt stock–recruit function and an M/K ratio of 1.65. Rows correspond to values of τ , the ratio of the age at 50% selectivity to the age at 50% maturity, and columns correspond to values of η_s , the slope of selectivity.



BRPs as a function of steepness, using knife-edged maturity, coincident knife-edged recruitment, and three different values each for M , K , and a_{MAT} . Clark (1991) considered shallower-sloped schedules in maturity and recruitment and the possibility of their offset using life-history parameters typical of New England groundfish. Goodyear (1993) analyzed SPR with life-history parameters describing Gulf of Mexico red snapper. Our study broadens the results from those previous by considering a full range of life-history parameters, the complete spectrum of steepness values, and an array of maturity and recruitment patterns. The analysis confirms that there is no single BRP value that can safely be applied to all stocks, a result that is only recently gaining consensus (Clark 2002; Dorn 2002; Myers et al. 2002).

The three reference points analyzed here, M based, B based, and SPR, do not constitute an exhaustive list. Even so, the methods here are general and could be used to investigate relationships between virtually any BRPs. Two others often used are F_{max} and $F_{0.1}$ (Sissenwine and Shepherd 1987). F_{max} is the fishing mortality rate that maximizes yield per recruit, and $F_{0.1}$ is the fishing mortality rate when the yield per recruit function has a slope of 10% of that at the origin. $F_{0.1}$ was originally proposed to be a more ecologically conservative reference than F_{max} , without too much sacrifice in yield (Gulland and Boerema 1973). However, both ignore effects

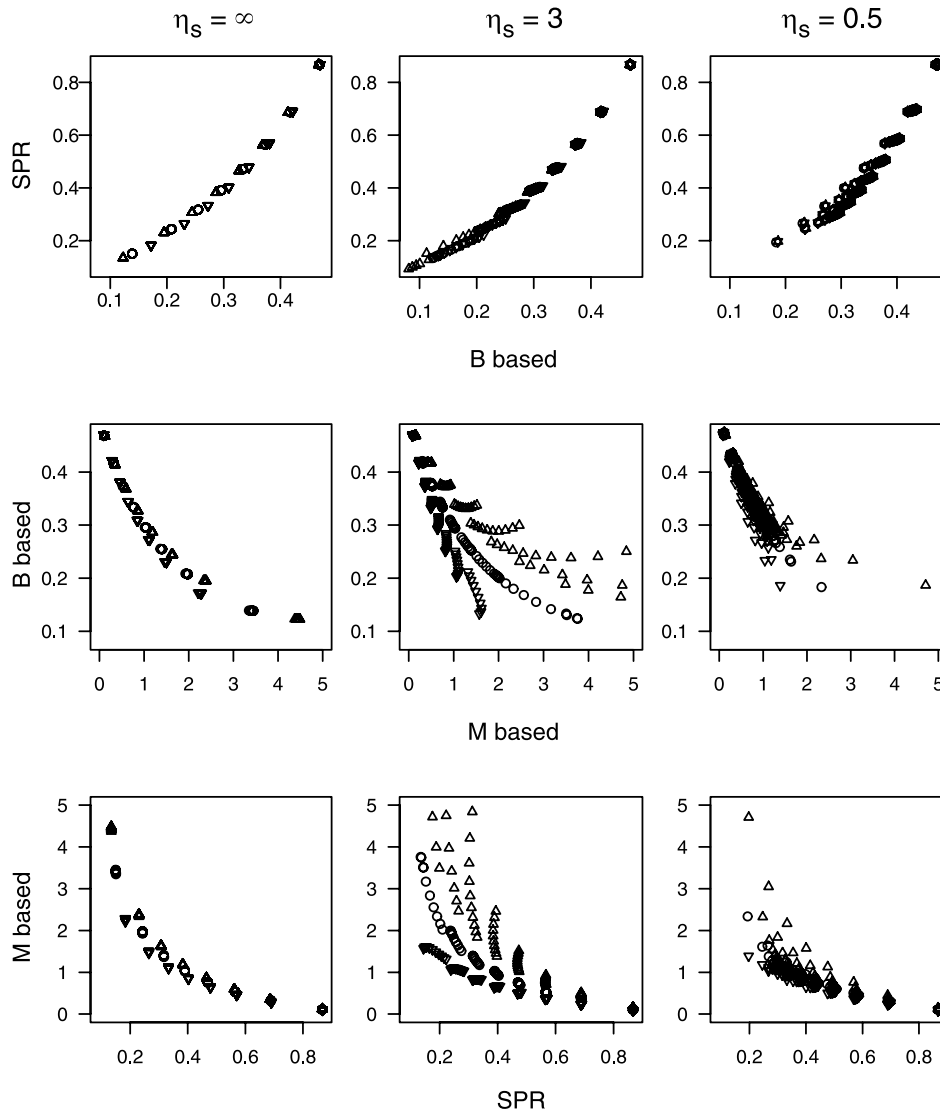
on the spawning population, and this can be dangerous (Quinn and Deriso 1999).

Of this paper's three BRPs, the M -based policy is the most sensitive to model parameters. Its applicability is limited to when the stock–recruit function is well determined and life history and steepness parameters are well estimated. Such conditions are rarely met, if ever. Natural mortality itself is particularly difficult to estimate accurately. In addition, the M -based BRP, like $F_{0.1}$ and F_{max} , ignores effects on spawning stock size. We recommend that M -based policies be eliminated from fishery management altogether.

The B -based and SPR BRPs do account for effects on the spawning population. Relative to the M -based policy, both are more robust to misspecifications in life-history parameters. The SPR BRP is nearly invariant with respect to life-history parameters M , K , and a_{MAT} . For these reasons, we advocate SPR as the BRP most likely to achieve management goals when life-history data are limited.

The results indicate potential inconsistencies in some harvest policies. For example, in the case of West Coast groundfish, the current proxy for B_{MSY} is a B -based proxy, $B_{40\%}$, defined as 40% of the unfished biomass size. Current management proxies for F_{MSY} for West Coast groundfish rely on SPR values ranging from $F_{40\%}$ to $F_{50\%}$, depending on the species group (PFMC 2001). Based on our analyses compar-

Fig. 5. Interrelationships of the M -based, B -based, and spawning potential ratio, SPR, biological reference points using the Beverton–Holt stock–recruit function and an M/K ratio of 1.65. Symbols refer to the value of τ , the ratio of the age when a cohort reaches 50% selectivity to the age at 50% maturity: $\tau = 0.75$, inverted triangle; $\tau = 1.0$, circle; and $\tau = 1.25$, triangle. For each value of τ , reference points are calculated for all combinations of steepness (incremented from 0.2 to 1.0) and the von Bertalanffy growth parameter (incremented from 0.1 to 1.0). Columns correspond to values of η_s , the slope of selectivity.



ing BRP values with each other, $B_{40\%}$ equates to SPR values of roughly $F_{65\%}$ and $F_{30\%}$ for the Beverton–Holt and Ricker stock–recruit functions, respectively. In either case, the proxies appear inconsistent if either function is assumed to underlie the population dynamics.

This study reiterates a fundamental message in fishery management: understanding the relationship between stock and recruitment is crucial. Very different BRP values emerge under the Beverton–Holt and Ricker functions, particularly for higher steepness values. With typical stock–recruit data, distinguishing between the two functions is no easy task. Judgment is often relegated to statistical software and based on which function provides a better fit to the data. In many data sets, those fits are driven by only a small number of data points with high stock size, where variability in recruitment is greatest. In such cases, distinction between the

Beverton–Holt and Ricker functions relies heavily on chance. This is risky given the disparate management implications stemming from the two functions. A better approach, we believe, is to choose a stock–recruit function a priori based on the presence or absence of biological mechanisms assumed by the model. Four examples of mechanisms that can lead to the dome shape of the Ricker function are adult cannibalism on juveniles, density-dependent disease transmission, density-dependent quality of spawning sites, and density-dependent growth accompanied by size-dependent mortality (Hilborn and Walters 1992). Unless good evidence supports a plausible mechanism for the Ricker function, the Beverton–Holt function is likely a better choice for management, especially given its more conservative BRP values.

In our analysis, we have assumed deterministic recruitment and survival. Other studies have examined the effects

Fig. 6. Interrelationships of the B -based and spawning potential ratio, SPR, biological reference points using the Beverton–Holt (solid) and Ricker (shaded) stock–recruit functions for various values of η_s , the slope of selectivity. For each panel, analyses use a range of values for K (0.025–1.0), M/K (0.5, 1.65, 2.5), and τ (0.75, 1.0, 1.25).

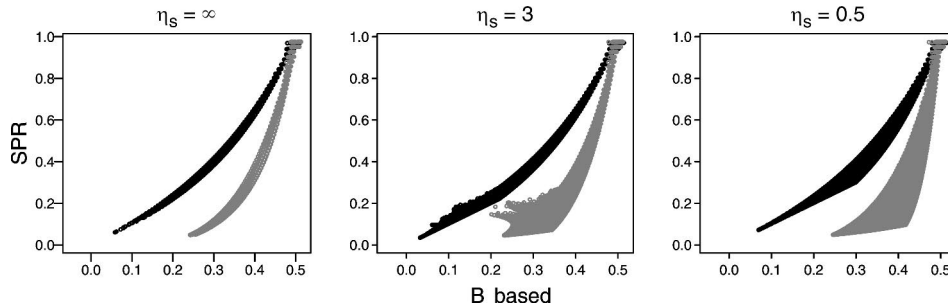
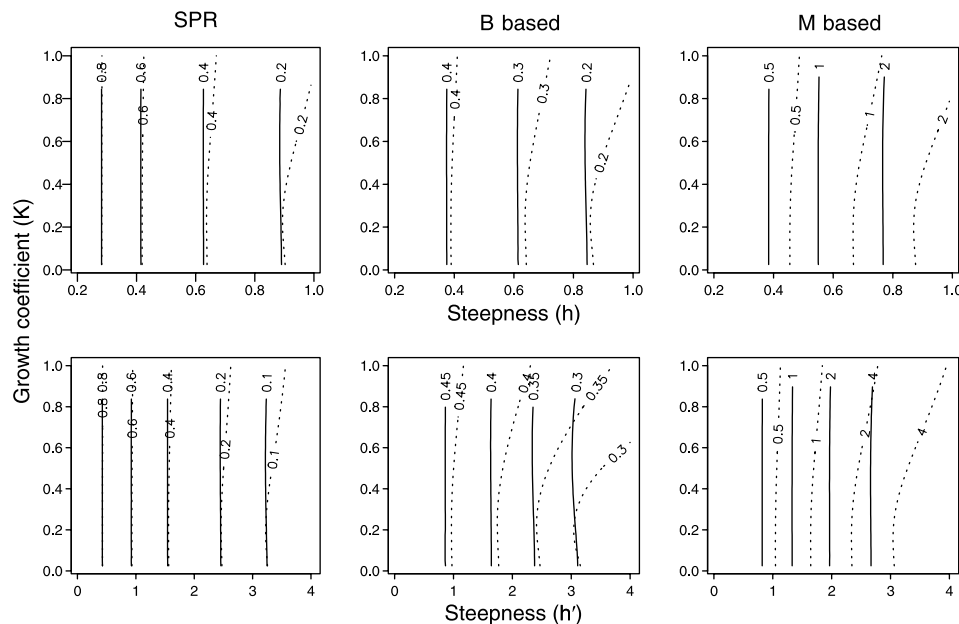


Fig. 7. Sensitivity of the spawning potential ratio (SPR), B -based, and M -based biological reference points to the M/K ratio under the Beverton–Holt (top row) and Ricker (bottom row) stock–recruit functions. Analyses use low (0.5, dotted line) and high (2.5, solid line) extremes of the M/K ratio. Other model specifications set at their intermediate values ($\tau = 1$ and $\eta_s = 3$).



of stochasticity on structured population models. Clark (1993) extended a previous study (Clark 1991) to include stochastic and serially correlated recruitment, resulting in higher recommended SPR. Tuljapurkar (1990) provided an approximation of the population growth rate for stochastic matrix models and noted that stochasticity often decreases the growth rate. Given those results, it is likely that by adding stochasticity to our analysis, similar BRP values would require higher steepness values. It is also likely that the relationship between BRPs and steepness would depend on the details of implementing stochasticity, such as the type(s) of random noise and correlation structure among parameters. Further research into the overall effects of stochasticity on BRPs is needed.

Ultimately, effective fishery management relies on obtaining some metric of the population growth rate. Steepness is a useful concept because it relates directly to population growth. It measures the maximum reproductive rate and, hence, the resilience of a stock to exploitation. Furthermore, steepness is comparable across stocks because it is inde-

pendent of selectivity, unlike F_{MSY} . Not surprisingly, all three BRPs are highly dependent on steepness. Our analysis can provide some understanding of the population growth rate or steepness implied when choosing an SPR proxy for management. Choosing a value of any BRP without regard to steepness would likely result in faulty management, and this implies that accurate estimation of steepness should be a top-priority goal. We recommend that BRPs be developed based on explicit assumptions about steepness.

How can steepness best be estimated when the stock–recruitment time series is of limited duration? The answer is not obvious, but carefully designed experiments and meta-analyses offer enticing possibilities (Myers and Barrowman 1996; Myers 2001). The optimal experimental design should, at a minimum, achieve reliable information about recruitment at high (virgin) and low (20% of virgin) SSB. Meta-analysis may be more feasible, averting the problem of a short time series by, in effect, substituting space for time. Multiple time series of spatially separated stocks, perhaps from different species with similar life histories, could be

Fig. 8. Values of biological reference points under the Beverton–Holt stock–recruit function and “knife-edged” selectivity, plotted for a range of steepness and M/K ratios. Columns correspond to values of τ , the ratio of the age at 50% selectivity to the age at 50% maturity.

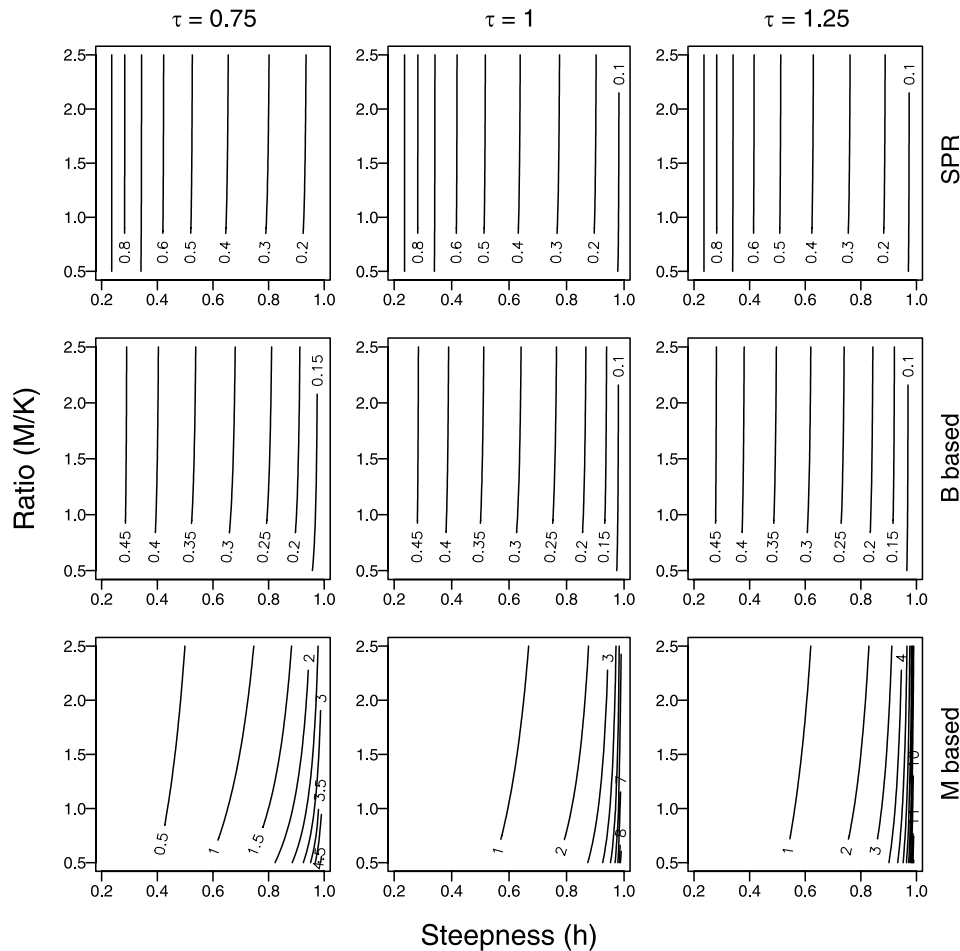
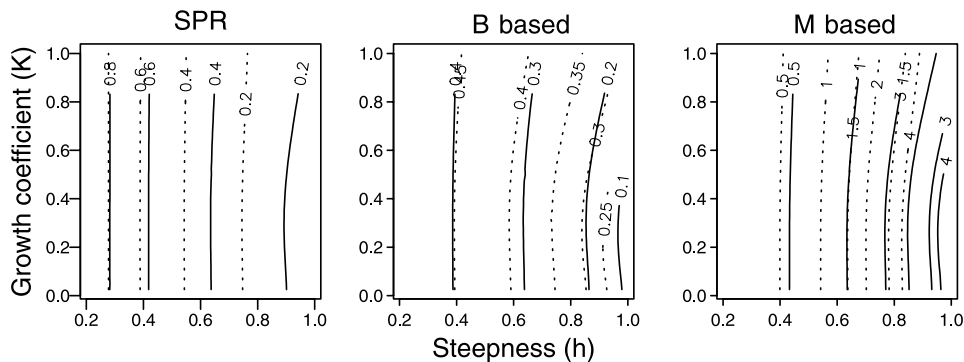


Fig. 9. Comparison of the spawning potential ratio (SPR), B -based, and M -based biological reference points under the Beverton–Holt (solid line) and Ricker (dotted line) stock–recruit functions. Ricker steepness is scaled to Beverton–Holt steepness by eq. 11. Other model specifications are set at their intermediate values ($\tau = 1$ and $\eta_s = 3$).



used as a surrogate for a single, longer time series. At the least, such an approach could be used to generate prior distributions of steepness for Bayesian analyses (McAllister et al. 2001; Myers et al. 2002). Distributions of steepness could also be used as input for the model here to generate probability distributions of BRPs.

Meta-analyses may also reveal correlations of steepness with biological and environmental factors. Myers et al. (2002)

examined several potential covariates and found a weak negative relationship between steepness and natural mortality, a seemingly contradictory relationship. As fisheries are depleted and rebuilt and stock–recruit databases improve, future meta-analyses may find stronger biological correlations on which to base management. However, further analyses may also reveal the opposite: that population growth rates for some stocks, as measured through steepness, are so strongly

linked to environmental and ecological conditions that management is better off acting on information from surveys of year-class strength than on BRPs assuming equilibrium conditions.

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